## Effect of Mixed-Salt Salinity on Growth and Ion Relations of a Barnyardgrass Species

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## ABSTRACT

Recent investigations of the plant genome have revealed a large degree of similarity among cereal crops (specifically within the family Triticeae) and other related grass species. Recognition of the close genetic relationship among the grasses indicates that more exotic species, such as weedy grasses, may be exploited by plant breeders to enhance biotic/abiotic stress tolerance in cereal crops. *Echinochloa crus-galli* (L.)[1] Beauv. (barnyardgrass), a wide-spread, persistent $C_4$ weed species of agricultural importance, is reported to tolerate high levels of salinity. Growth and ion relations were studied in barnyardgrass using mixed-salt salinity (with final electrical conductivities (ECi) of 3 (control), 7, 11, and 19 dS m$^{-1}$ in the irrigation water) to determine whether the mechanism(s) for its salt tolerance are similar to those previously reported for other cereal crops. Such a finding would indicate that barnyardgrass may possess valuable genetic traits. Ion accumulation and ion selectivity ratios in the various treatments were determined from oven-dried shoot tissue. Significant (P < 0.01) linear regressions were obtained between either fresh weight or plant height and ECi. The point of 50% reduction ($C_{50}$) in fresh weight was predicted to occur at about 13.9 dS m$^{-1}$; the $C_{50}$ value for plant height was at about 22.9 dS m$^{-1}$. Statistical analysis of calculated Gapon constants for potassium (K)/sodium (Na) indicated that ion selectivity was not affected until after 11 dS m$^{-1}$. Calcium (Ca)/Na selectivity was not significantly affected by salinity. We concluded that, similar to some cereal crops, barnyardgrass maintains growth under

[1]Mention of company names or products is for the benefit of the reader and does not imply endorsement, guarantee, or preferential treatment by the USDA or its agents.

saline conditions by maintaining high K/Na ratios, possibly because of better membrane integrity due to high Ca selectivity.

**Keywords:** *Echinochloa crus-galli* (L.), weed, salinity, salt stress, salt tolerance, ions

## INTRODUCTION

High-quality water needed for agriculture is becoming increasingly scarce due to changing environmental standards and rising demands from urban areas. Any future expansion of irrigated agricultural production will need to include the use of waters containing higher levels of soluble salts. Unfortunately, salt-induced growth suppression is already a major obstacle to crop production on saline lands, as most irrigation systems currently used suffer from the effects of salinity. Although accurate data are lacking, the Food and Agriculture Organization (FAO) and the United Nations Educational, Scientific and Cultural Organization (UNESCO) have estimated that one-half of the world's existing irrigation systems are seriously affected by salinity (Szabolcs, 1985). Thus, the development of more salt-tolerant crops will become more important as the balance between food supply and demand becomes more delicate as human populations increase.

Unfortunately, two of the world major cereals, rice (*Oryza sativa* L.) and corn (*Zea mays* L.) are sensitive to salts in the root zone (Maas, 1990). This is somewhat surprising in that most of the major cereals belonging to the grass family show moderate to high salt tolerance (Maas, 1990). The grass family is very large and contains grater physiological, morphological, and genetic diversity than just the major cereal crops. Other grasses, then, may serve as a source of useful genetic traits for these grasses.

Recent investigations of the plant genome have revealed extensive similarities among the cereal crops and other grass species, such that a gene on the chromosome of one species can be anticipated to be present in a predicted location on a specific chromosome of a number of other grass family species (Kellogg, 1998; Messing and Llaca, 1998; Phillips and Freeling, 1998). Recognition of the close genetic relationship among the grasses indicates that more exotic species such as weedy grasses may possess valuable genetic information that the plant breeder may exploit in growing important cereal crops, such as rice and corn.

In an earlier study of growth responses in *Echinochloa crus-galli* (barnyardgrass) under saline conditions, Aslam et al. (1987) reported a 50% reduction in shoot dry matter at about 15.9 dS m$^{-1}$. They suggested that the high salt tolerance observed in barnyardgrass may be due to its ability to selectively absorb potassium (K$^+$) at high salinity, though no direct evidence was presented to support their conclusion. More recently, Rahman and Ungar (1994) reported a 79% reduction in shoot dry-matter accumulation when barnyardgrass was grown under a 1% NaCl treatment. These two reports are consistent because a 1% NaCl solution alone would have an electrical conductivity (EC) of about

17.5 dS m$^{-1}$, and plant nutrients would contribute about 1 dS m$^{-1}$ to treatment EC, for a sum of 18.5 dS m$^{-1}$ EC in the irrigation water.

Because the ability to maintain relatively high K/sodium (Na) ratios and calcium (Ca) selectively is believed to be an important salt-tolerance mechanism in many crop species (Grieve and Maas, 1988), it is important to find that salt tolerance in barnyardgrass can be attributed in part to selective absorption of K$^+$. Such a finding would suggest weedy species represent a large germplasm base that may be exploited to further understand the mechanism(s) of plant salt tolerance.

Thus, in the present study we investigated whether or not the relatively high salt tolerance in *E. crus-galli* is related to its ability selectively to absorb K$^+$. To accomplish this, we used a typical saline water mixture, of mixed-salt, sodium sulfate, and chloride salinity, to study the growth response of *E. crus-galli* L. (Beauv.). This form of salinity is prevalent in drainage waters from irrigated agriculture in the San Joaquin Valley of California, where barnyardgrass is a pest. We calculated the K/Na selectivity ratios ($S_{K,Na}$) from the ion data according to Pitman (1976). Because the properties of the root-shoot apoplastic space are modified by changes in the cell wall matrix (Läuchli, 1976) and thus may influence final ion levels in the shoot, we also employed the Gapon convention suggested by Suarez and Grieve (1988). Analysis of these data supports the hypothesis presented by Aslam et al. (1987), that salt tolerance of barnyardgrass is due to its ability to maintain relatively high K/Na ratios, possibly resulting from sustained Ca-Na selectivity.

## MATERIALS AND METHODS

### Plant Material and Salinity Treatments

The experiment was conducted under natural sunlight in a greenhouse located at the George E. Brown Jr. Salinity Laboratory, Riverside, CA (lat 33°, 58′ N long 117°, 21′ W). Temperature settings of 28°C day and 18°C night were controlled by evaporative coolers and heaters, while relative humidity in the greenhouse was uncontrolled. Seed of *E. crus-galli* (Valley Seed Service, Fresno, CA) was sown at a depth of 5–10 mm on October 31, 1997 into 24 sand tanks (each 1.2 × 0.6 × 0.5 m deep). The tanks contained a washed-coarse sand with an average bulk density of 1.2 mg m$^{-3}$ and an average volumetric water content of 0.34 m$^3$ m$^{-3}$ at saturation. Each treatment-replication combination comprised two rows spaced 10 cm apart with plants spaced 3.8 cm within each row, for 15 plants per row. Plants were irrigated twice daily with a nutrient solution containing the following (in mM): 2.5 Ca$^{2+}$, 1.25 Mg$^{2+}$, 15 Na$^+$, 3 K$^+$, 6.0 SO$_4^{2-}$, 7.0 Cl$^-$, 5.0 NO$_3^-$, 0.17 KH$_2$PO$_4$, 0.050 Fe as sodium ferric diethylenetriamine pentaacetate (NaFeDTPA), 0.023 H$_3$BO$_3$, 0.005 MnSO$_4$, 0.0004 ZnSO$_4$, 0.0002 CuSO$_4$, and 0.0001 H$_2$MoO$_4$ made up with City of Riverside, CA, municipal water.

This base nutrient solution ($EC_i = 3.0\,dS\,m^{-1}$) served as the control treatment throughout the experiment and to establish seedlings. Irrigation waters were contained in separate 765 L reservoirs located in the basement of the greenhouse. Each irrigation was 10 min in duration, which allowed the sand to become completely saturated, after which the solution drained back into the reservoirs for reuse in the next irrigation.

A difference certainly exists between salinity studies conducted in sand culture and those performed under natural soil conditions. We also recognize two major difficulties that must be addressed when using high-sulfate salinity investigations in sand culture. First, in soils the relative proportions of sulfate salts ($CaSO_4/Na_2SO_4$) change with the total salt levels. Thus, detailed calculations were required to estimate the amounts of $MgSO_4$ and $Na_2SO_4$ needed to achieve given EC values in our irrigation waters. In order to deal with this problem, we used irrigation water formulations that simulated the saline drainage water usually found in the San Joaquin Valley of California and compositions of higher salinity that would result from the concentration of these waters (Suarez and Šimůnek, 1997). In such formulations, $Na^+$, $SO_4^{2-}$, $Cl^-$, and $Mg^{2+}$ are the predominant ions. Second, Ca concentrations vary due to calcite and gypsum precipitation. In order to correct for the effects of precipitation, the $Ca^{2+}/Mg^{2+}$ ratio was decreased proportionally as salinity increased. Salinization treatments commenced on November 4, when plants had reached the two-leaf stage of development. Equivalent amounts of salts were added over a 4 d period to avoid osmotic shock to the seedlings. The final electrical conductivities of the irrigation waters ($EC_i$) were: 3 (control), 7, 11, and 19 dS m$^{-1}$. The pH of the solutions was not controlled and ranged from 7.7 to 8.0 across treatments. The irrigation waters were analyzed weekly using inductively coupled plasma optical emission spectrometry (ICPOES) to confirm that target ion concentrations were maintained. Ion compositions are shown in Table 1.

Plants were harvested on December 18, 44 d following salinization, because more than 75% of the plants were at the jointing or booting stage of development, having completed their vegetative growth phase. We determined height to the

Table 1
Composition of mixed-salt solutions used to irrigate *E. crus-galli*[a]

| Salinity Level | (meq L$^{-1}$) | | | | | |
|---|---|---|---|---|---|---|
| | Ca | Mg | Na | K | SO$_4$ | Cl |
| (dS m$^{-1}$) | | | | | | |
| 3 (control) | 7.0 | 4.9 | 21.5 | 2.4 | 21.8 | 10.6 |
| 7 | 14.6 | 11.5 | 50.9 | 3.4 | 51.7 | 24.7 |
| 11 | 20.3 | 19.6 | 87.0 | 3.9 | 84.0 | 42.2 |
| 19 | 26.9 | 37.9 | 167.8 | 5.6 | 150.4 | 81.3 |

[a]Plants were irrigated twice daily.

tallest leaf from 10 central plants in each row, cut these plants at the soil surface, and determined above-ground fresh weights. Leaf area of five randomly selected plants was determined using a LI-3000 leaf area meter (Li-Cor, Lincoln, NE). Plant tissues were dried at 60°C to a constant weight and weighed. Values for fresh weight, leaf area, and dry-weight accumulation are expressed on a per-plant basis.

## Plant Ion Analysis

Harvested shoots were rinsed for 10–20 s in deionized water, blotted dry on paper towelling, dried at 60°C, their dry weight was then determined. Oven-dried tissue was subsequently ground and stored in acid-washed vials. Total S, total P, $Ca^{2+}$, $Mg^{2+}$, $Na^+$, and $K^+$ were measured on nitric-perchloric acid digests of shoot tissue by ICPOES. Chloride was determined by coulometric-amperometric titration. Shoot samples were analyzed for total nitrogen (N) by standard micro-Kjeldahl methods.

## Experimental Design and Statistical Analysis

The fixed arrangement of 24 sand tanks and associated irrigation equipment (reservoirs, pipe, and pumps) was such that three tanks were irrigated from a common 765 L reservoir. Therefore, the experimental design comprised two 'true' replicates for statistical analysis, that is, six sand tanks at each of four salinity levels. In order to minimize covariance in the treatment structure, we assigned the eight reservoirs (i.e., two for each main effect of salinity at 3, 7, 11, and 19 dS $m^{-1}$) as nearly as possible to achieve a randomized complete block design in the 24 sand tanks in the greenhouse. This arrangement resulted in five blocks positioned parallel to one another in a north-south orientation, whereas the sixth block of tanks was nested in the southernmost side of the greenhouse and oriented in an east-west direction. A model employing subsamples from each of three sand tanks revealed no gain in efficiency compared with experimental error variance (data not shown). Accordingly, the experimental design was a randomized block with six replicates. Data were subjected to (1) analysis of variance and means separated by the least significant difference (LSD) at the 5% level of probability, and (2) linear and nonlinear regression analyses in order to determine the best-fit salt-tolerance model as described by van Genuchten and Hoffman (1984) using SAS procedures (SAS Institute, 1997).

## RESULTS

### Growth Responses

Shoot fresh weight and plant height of barnyardgrass decreased significantly ($P < 0.05$) across the four salinity levels (Table 2). Salinity stress led to

Table 2

Effects of mixed-salt salinity on selected growth characteristics and plant N and P concentration in *E. crus-galli*

| Salinity level (dS m$^{-1}$) | Fresh wt. (g) | Height (cm) | Leaf area (cm$^2$) | Plant [N] (g kg$^{-1}$) | Plant [P] (mmol kg$^{-1}$) |
|---|---|---|---|---|---|
| 3 (Control) | 2.07 (0.32) | 53.4 (4.0) | 40.8 (5.7) | 29.9 (0.4) | 187.5 (22.7) |
| 7 | 1.31 (0.14) | 46.9 (1.8) | 28.8 (3.4) | 27.7 (1.0) | 148.5 (25.0) |
| 11 | 1.37 (0.34) | 45.2 (5.0) | 31.5 (6.0) | 26.7 (1.4) | 150.7 (36.7) |
| 19 | 0.71 (0.09) | 32.8 (2.7) | 24.3 (2.5) | 29.0 (1.4) | 145.1 (31.1) |

[a]Values are means of 10 plants from six replicate tanks ($\pm 1$ standard error of the mean).

reductions somewhat larger in fresh weight than in height, but a strong association was obtained between these two traits ($r^2 = 0.96$, P < 0.05). Variation in leaf area, shoot N, and shoot P was not significant; however, values for leaf area and P were numerically lower in plants at 19 dS m$^{-1}$ than in controls. Standard error values were largest among plants grown at 11 dS m$^{-1}$, suggesting that variability in plant growth responses to salinity compromised our detection of statistically significant difference in leaf area, plant N, and P.

Across the four salinity treatments, salt tolerance appeared to be adequately described by a quadratic function (van Genuchten and Hoffman, 1984); however, in no instance was the quadratic term significant (P > 0.50, data not presented). Analysis of simple linear regression between shoot fresh weight and salinity level indicated a highly significant (P < 0.002, n = 24) linear relationship, with a coefficient of determination ($r^2$) of 0.46, a slope coefficient of $-0.076$ g fresh weight per dS m$^{-1}$ (SE = 0.018), and a predicted C$_{50}$ value of about 13.9 dS m$^{-1}$. The linear salt tolerance model for plant height had an $r^2 = 0.53$, a slope coefficient of $-1.24$ g dS m$^{-1}$ (SE = 0.018), and a predicted C$_{50}$ value of about 22.9 dS m$^{-1}$. These results support data in Table 2 showing that height was more salt tolerant than fresh weight. Plant height appears to be an important weedy characteristic of barnyardgrass, and may confer competitive advantage in some cropping systems (Maun and Barrett, 1986).

## Ion Analysis

Aslam et al. (1987) suggested that the high salt tolerance of barnyardgrass may be due to its abililty selectively to absorb K$^+$ under conditions of high salinity. In accordance with this hypothesis, our analysis of ion composition in shoot tissues indicates that barnyardgrass maintained high K$^+$ levels relative to Na$^+$ content (Table 3). From these data, the K/Na selectivity ratios ($S_{K,Na}$) were

Table 3

Mineral composition in whole shoots of *E. crus-galli* grown for 44 d at four levels of mixed-salt salinity in the irrigation waters

| Salinity Level | (mmol kg$^{-1}$ dry weight) | | | | | |
|---|---|---|---|---|---|---|
| | Ca | Mg | Na | K | S | Cl |
| (dS m$^{-1}$) | | | | | | |
| 3 | 168 (9)[a] | 625 (31) | 69 (20) | 1066 (39) | 281 (26) | 704 (44) |
| 7 | 167 (5) | 641 (35) | 91 (13) | 970 (38) | 290 (19) | 706 (51) |
| 11 | 156 (6) | 659 (26) | 119 (20) | 868 (45) | 318 (28) | 711 (72) |
| 19 | 128 (11) | 655 (21) | 189 (29) | 895 (57) | 342 (26) | 668 (52) |

[a]Values are means of 10 plants from six replicate tanks ($\pm 1$ standard error of the mean).

calculated following Pitman (1976), where

$$S_{K,Na} = (K \text{ content}/[K] \text{ medium}):(Na \text{ content}/[Na] \text{ medium}). \tag{1}$$

A number of studies suggest K/Na selectivity may be important in salinity tolerance (Binzel and Reuveni, 1994; Flowers et al., 1977; Jeschke, 1984; Rains, 1972). The $S_{K,Na}$ values for barnyardgrass grown at 3, 7, 11, and 19 dS m$^{-1}$ were 193, 160, 163, and 142, respectively. These results support our earlier contention that barnyardgrass can maintain relatively high K$^+$ selectivity at high external Na$^+$ levels.

Adams (1966) suggested plant response is more closely related to the external activity of an ion rather than its concentration. Moreover, Läuchli (1976) reported that the properties of the root-shoot apoplastic space are modified by charges in the cell-wall matrix. In fact, the xylem cylinder has been visualized as an ion-exchange column that can influence the upward movement of ions by a series of exchange reactions on the negatively charged walls (Bell and Biddulph, 1963; Demarty et al., 1984; Knight et al., 1961; van de Geijin and Petit, 1979). This concept led Suarez and Grieve (1988) to suggest that the principles of ion-exchange theory could be used to investigate cation uptake and transport.

Using the Gapon convention suggested by these authors, we examined barnyardgrass preference for various ion combinations (Table 4). The data are expressed using the Gapon selectivity constant (K$_g$), which relates the equivalent fractions of the exchange ions to the activities of the ions in solution (Sposito, 1981). For K-Na exchange the constant is expressed as follows:

$$K_g = E_{Na} \cdot a_K / (E_K \cdot (a_{Na})^{0.5}) \tag{2}$$

In general, the calculated K$_g$ values follow the same pattern as $S_{K,Na}$. The large K$_g$ value for K-Na at 3 dS m$^{-1}$ (control) indicates that the cation uptake process

Table 4

Effects of mixed-salt salinity on Gapon constants in *E. crus-galli* calculated according to Equation 2

| Salinity Level | ($K_{Gapon}$) | | |
|---|---|---|---|
| | Ca/Na | Mg/Ca | K/Na |
| (dS m$^{-1}$) | | | |
| 3 | 1.49 (0.12) | 6.15 (0.40) | 216 (15) |
| 7 | 1.40 (0.30) | 5.54 (0.16) | 182 (20) |
| 11 | 1.71 (0.28) | 4.82 (0.28) | 183 (25) |
| 19 | 1.17 (0.05) | 4.21 (0.36) | 120 (6) |

[a] Values for $K_{Gapon}$ Ca/Na grown at 7dS m$^{-1}$ are means of 10 plants from three replicate tanks; otherwise, of 10 plants from six replicate tanks ($\pm 1$ standard error of the mean).

in barnyardgrass has a large preference for K$^+$. We found $K_g$ remained nearly constant as salinity increased up to 11 dS m$^{-1}$, and then decreased significantly at 19 dS m$^{-1}$ (P < 0.02).

Because the Ca-nutritional status of plants may be strongly influenced by ionic composition in the external media (Bernstein,1975; Cramer and Läuchli, 1986; Cramer et al., 1986; Fageria, 1983; Suhayda et al., 1992), we calculated $K_g$ for both Ca Na selectivity and Mg Ca selectivity (Table 4). As was observed for K Na selectivity, barnyardgrass maintained Ca Na selectivity to 11 dS m$^{-1}$, after which point we measured a decrease, although it was not significant (P > 0.08). With respect to Mg Ca, selectivity was quickly reduced under salt stress; we noted a significant decrease at 7 dS m$^{-1}$ (P < 0.01).

## DISCUSSION

The present study investigated the effect of a mixed-salt salinity typical of San Joaquin Valley drainage waters on the growth of the C$_4$ weed *Echinochloa crus-galli* (barnyardgrass). These waters are characterized by high pH (around 8.0) and low Ca solubility. The data were analyzed for derivation of salt-tolerance functions according to published approaches (Maas and Hoffman, 1977; van Genuchten and Hoffman, 1984; Maas, 1990); however, best-fit curves were obtained using simple linear regression. Accordingly, the point at which fresh weight of barnyardgrass was reduced 50% (C$_{50}$) by mixed-salt salinity was at about 13.9 dS m$^{-1}$. Similarly, in studies of barnyardgrass grown in a high NaCl system, Aslam et al. (1987) found that a 50% decrease in dry matter would occur at 15.9 dS m$^{-1}$. Our results also are in agreement with those reported by Bilski and Foy (1988), though any direct comparison of C$_{50}$ values is complicated by the fact that these investigators reported salinity levels in milligrams salt (NaCl or Na$_2$SO$_4$) per kilogram peat. According to the values listed by Maas (1986),

our $C_{50}$ value for barnyardgrass is much higher than for many crops such as salt-sensitive rice (3.6 dS $m^{-1}$), and is close to that reported for wheat (13.0 dS $m^{-1}$), a moderately tolerant species.

It is interesting that plant height was somewhat less sensitive to salinity (with $C_{50}$ of about 23 dS $m^{-1}$) than shoot fresh weight ($C_{50}$ of about 14 dS $m^{-1}$). An investigation into resource allocation was beyond the scope of this research, but one possible explanation for this observation is that resources allocated to fresh-weight growth were redirected to maintain height under high salinity. This possibility is supported, insofar as the literature is concerned, only by Maun and Barret (1986), who suggest that much of the competitive success of barnyardgrass is due to its ability to grow rapidly. The ability to grow faster initially and to shade other species may be important for both reproductive and competitive success (Pearcy et al., 1981). Thus, shifting of resources towards increased plant height may be an important adaptation to plant stress, and if this allometric is indeed achieved in barnyardgrass, then perhaps investigations of salinity stress in weedy species should focus on growth parameters important to the weed's competitive success (e.g., rate of development) rather than parameters normally used in investigations of crops plants, such as final economic yield.

This present study and a previous investigation of wheat genotypes (Omielan et al., 1991) suggest salt tolerance in grass species is closely related to the selectivity of K over Na. In barley (*Hordeum vulgare* L.), the relationship between tissue K/Na ratio and salinity tolerance was strong enough to propose that it may serve as a selection criterion in breeding salt-tolerant genoptypes. Our data agree with these proposals and support the hypothesis of Aslam et al. (1987) that K selectivity is an important factor in the salt tolerance of barnyardgrass. Plant selectivity for K, as measured by the $K_g$, did not change from control levels up to and including 11 dS $m^{-1}$, after which point it decreased (Table 4). This decrease coincided with a decrease in plant height at high salinity (Table 2).

The marked decreases in plant height (Table 2) and in $K_g$ for Na-K at 19 dS $m^{-1}$ coincided with a decrease in $K_g$ for Ca/Na between 11 and 19 dS $m^{-1}$ (Table 4). One possible explanation for this observation is that salt tolerance of barnyardgrass is associated with relatively high tissue K/Na ratios, due to its ability to maintain a better membrane integrity from sustained Ca/Na selectivity at salinity levels of about 11 dS $m^{-1}$. Low K/Na and Ca/Na ratios in irrigation waters have been shown to reduce the ion selectivity of root membranes (Kramer et al., 1977). Similarly, Bernstein (1975) reported that Ca concentrations deemed adequate under non-saline conditions may not be adequate (i.e., become limiting) for plant function in a saline environment, due to a combination of limited root growth and the inhibition of Ca transport from root to shoot. Further, Cramer et al. (1986) and Cramer and Läuchli (1986) reported that high levels of external Na can significantly reduce the activity of Ca in the root media and subsequently decrease Ca uptake. Our results for

Ca-ion selectivity are consistent with the findings of Suhayda et al. (1992), who reported that Ca had a positive effect on K/Na selectivity in salt-tolerant barley. However, this potential salt-tolerance mechanism must remain tentative in barnyardgrass, as the decrease in the $K_g$ for Ca Na at 19 dS m$^{-1}$ was not highly significant (P > 0.08; 5% LSD = 0.74).

Mixed-salt salinity did not significantly alter P and N status of the plant. Although other studies report decreased N in salt-stressed plants (Aslam et al., 1984; Torres and Bingham, 1973), our mixed-salt solutions contained relatively low levels of chloride (Cl), and some evidence suggests Cl ions compete with $NO_3$ for binding sites on the plasma membrane, and thereby reduce the uptake and transport of $NO_3$ in the plant (Marschner, 1986). Of particular interest was the observation that while the concentration of Cl in the external media increased eight-fold (Table 1), Cl levels in the shoot essentially remained constant (Table 2). Aslam et al. (1987) reported only a small increase in Cl levels in barnyardgrass as NaCl salinity increased from 3 dS m$^{-1}$ to 20 dS m$^{-1}$. Our current level of understanding of the Cl transport indicates that there may exist a weak antagonistic relationship between sulfate and chloride ions (Elzam and Epstein, 1965; Murarka et al., 1973; Schnug, 1990). Such a relationship may be operating in barnyardgrass, as evidenced by the small, but significant increase in S with increasing salinity (Table 3).

Apparently, the ability to maintain high K/Na ratios and Ca selectivity in crops such as barley, wheat, and some genotypes of sorghum (*Sorghum bicolor*) (Grieve and Maas, 1988) is also important in barnyardgrass. These findings also indicate that some weedy grass species may represent a germplasm base that may be exploited to further understand and alter the mechanism(s) of plant salt tolerance for enhanced production of crops in saline environments.

Certainly, the germplasm chosen for the present study may not fully represent the weed complex of barnyardgrass encountered in the field; however, we believe that our study of mixed-salt salinity, typical of San Jaoquin Valley drainage water, provides general knowledge of the strategies employed by a salt-tolerant species for regulating ionic and osmotic environments.

### ACKNOWLEDGMENTS

### REFERENCES

Adams, F. 1966. Calcium deficiency as a causal agent of ammonium phosphate injury to cotton seedlings. *Proceedings of the Soil Science Society of America* 30: 485–488.

Aslam, M., R. C. Huffaker, and D. W. Rains. 1984. Early effects of salinity on nitrate assimilation in barley seedlings. *Plant Physiology* 76: 321–325.

Aslam, Z., M. Salimn, R. H. Qureshi, and G. R. Sandhu. 1987. Salt tolerance of *Echinochloa crusgalli. Biologia Plantarum* (Praha) 29: 66–69.

Bell, C.W., and O. Biddulph. 1963. Translocation of calcium. Exchange versus mass flow. *Plant Physiology* 38: 610–614.

Bernstein, L. 1975. Effects of salinity and sodicity on plant growth. *Annual Review of Phytopathology* 13: 295–312.

Bilski, J. J., and C. D. Foy. 1988. Differential tolerances of weed species to aluminum, manganese and salinity. *Journal of Plant Nutrition* 11: 93–105.

Binzel, M. L., and M. Reuveni. 1994. Cellular mechanisms of salt tolerance in plant cells. *Horticultural Review* 16: 33–69.

Cramer, G. R., and A. Läuchli. 1986. Ion activities in solution in relation to $Na^+$-$Ca^{2+}$ interactions at the plasmalemma. *Journal of Experimental Botany* 37: 320–330.

Cramer, G. R., A. Läuchli, and E. Epstein. 1986. Effects of NaCl and $CaCl_2$ on ion activites in complex nutrient solutions and root growth of cotton. *Plant Physiology* 81: 792–797.

Demarty, M., C. Morvan, and M. Thellier. 1984. Calcium and the cell wall. *Plant, Cell Environment* 7: 441–448.

Elzam, O. E., and E. Epstein. 1965. Absorbtion of chloride by barley roots: Kinetics and selectivity. *Plant Physiology* 40: 620–624.

Fageria, N. K. 1983. Ionic interactions in rice plants from dilute solutions. *Plant and Soil* 70: 309–316.

Flowers, T. J., P. F. Troke, and A. R. Yeo. 1977. The mechanisms of salt tolerance in nonhalophytes. *Annual Review in Plant Physiology* 28: 89–121.

Grieve, C. M., and E. V. Maas. 1988. Differential effects of sodium/calcium ratio on sorghum genotypes. *Crop Science* 28: 659–665.

Jeschke, W. D. 1984. $K^+$-$Na^+$ exchange at cellular membranes intracellular compartmentation of cations and salt tolerance. In *Salinity tolerance in plants: Strategies for crop improvement*, 1st edition, eds. R. C. Staples and G. H. Toenniess, 34–66. New York: John Wiley.

Kellogg, E. A. 1998. Relationships of cereal crops and other grasses. *Proceedings of the National Academy of Sciences* 95: 2005–2010.

Knight, A. H., W. M. Crooke, and R. H. E. Inkson. 1961. Cation-exchange capacity of tisues of higher and lower plants and their related uronic acid content. *Nature* 192: 142–143.

Kramer, D., A. Läuchli, A. R. Yeo, and J. Gullasch. 1977. Transfer cells in roots of *Phaseolus coccineus*: Ultra-structure and possible function in exclusion of sodium from the shoot. *Annuals of Botany* 41: 1031–1040.

Läuchli, A. 1976. Apoplastic transport in tissues. In *Encyclopedia of plant physiology, transport in plants: Tissues and organs*, eds. U. Lüttge and M. G. Pitman, Vol. 2B, 1–34. New York: Springer-Verlag.

Maas, E. V. 1986. Salt tolerance of plants. *Applied Agricultural Research* 1: 12–26.

Maas, E. V. 1990. Crop tolerance. In *Agricultural salinity assessment and management*, ed. K. K. Tanji, Practice No. 71, 262–304, ASCE Manuals. New York: Report on Engineering, American Society of Civil Engineers.

Maas, E. V., and G. J. Hoffman. 1977. Crop salt tolerance: Current assessment. *Journal of Irrigation and Drainage* (Division of American Society of Civil Engineers) 103: 115–1314.

Marschner, H. 1986. *Mineral nutrition in higher plants*, 39. London: Academic Press.

Maun, M. A., and S. C. H. Barrett. 1986. The biology of Canadian weeds, *Echinochloa crus-galli* (L.) Beauv. *Canadian Journal of Plant Science* 66: 739–759.

Messing, J., and V. Llaca. 1998. Importance of anchor genomes for any plant genome project. *Proceedings of the National Academy of Science* 95: 2017–2020.

Murarka, I. P., T. L. Jackson, and D. P. Moore. 1973. Effects of N, K, and Cl on nitrogen components of Russet Burbank potato plants (*Solanum tuberosum* L.). *Agronomy Journal* 65: 868–870.

Omielan, J. A., E. Epstein, and J. Dvorak. 1991. Salt tolerance and ionic relations of wheat as affected by individual chromosomes of salt-tolerant *Lophopyrum elongatum*. *Genome* 34: 961–974.

Pearcy, R. W., N. Tumosa, and K. Williams. 1981. Relationships between growth, photosynthesis and competitive interactions for a $C_3$ and $C_4$ plant. *Oecologia* 48: 371–376.

Phillips, R. L., and M. Freeling. 1998. Plant genomics and our food supply. *Proceedings of the National Academy of Sciences* 95: 1969–1970.

Pitman, M. G. 1976. Ion uptake by plant roots. In *Encyclopedia of plant physiology transport in plants. II. Part B. Tissues and organs*, eds. U. Lüttge and M. G. Pitman, Vol. II, 95–128. Berlin: Springer-Verlag.

Rahman, M., and I. A. Ungar. 1994. The effect of competition and salinity on shoot growth and reproductive biomass of *Echinochloa crus-galli*. *Aquatic Botany* 48: 343–353.

Rains, D. W. 1972. Salt transport by plants in relation to salinity. *Annual Review in Plant Physiology* 23: 367–388.

SAS Institute. 1997. SAS/STAT Software: Changes and enhancements through release 6.12. Cary, NC: SAS Institute.

Schnug, E. 1990. Sulfur nutrition and quality of vegetables. *Sulfur in Agriculture* 14: 3–7.

Sposito, G. 1981. The thermodynamics of soil solutions. Oxford: Oxford University Press.

Suarez, D. L., and C. M. Grieve. 1988. Predicting cation ratios in corn from saline solution composition. *Journal of Experimental Botany* 39: 605–612.

Suarez, D. L., and J. Šimůnek. 1997. UNSATCHEM: Unsaturated water and solute transport model with equilibrium and kinetic chemistry. *Soil Science Society of America Journal* 61: 1633–1646.

Suhayda, C. G., R. E. Redmann, B. L. Harvey, and A. L. Cipywnyk. 1992. Comparative response of cultivated and wild barley species to salinity stress and calcium supply. *Crop Science* 32: 154–163.

Szabolcs, I. 1985. Salt affected soils, as world problem. In *Proceedings of the reclamation of salt-affected soils international symposium*, 30–47. Jinan, China: Bejing Agricultural University.

Torres, B. C., and F. T. Bingham.1973. Salt tolerance of Mexican wheat. 1. Effect of $NO_3$ and NaCl on mineral nutrition, growth, and grain production of four wheats. *Proceedings of the Soil Science Society of America* 37: 711–715.

van de Geijn, T., and C. M. Petit. 1979. Transport of divalent cations. *Plant Physiology* 64: 954–958.

van Genuchten, M. T., and G. J. Hoffman. 1984. Analysis of crop salt tolerance data. In *Soil salinity under irrigation: Processes and management*, eds. I. Shainberg and J. Shalhevet, 258–271. Berlin: Springer Verlag.